
PLANT NATURALIZATIONS AND INVASIONS IN THE EASTERN UNITED STATES: 1634–1860¹

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ABSTRACT

Plant immigrants to North America arrived from Europe with the first human immigrants, products of the intense incentive early colonists felt to transplant European agriculture into the Western Hemisphere. Among early deliberate and accidental introductions were species that would soon become naturalized in eastern North America: *Artemisia absinthium*, *Hyoscyamus niger*, *Plantago lanceolata*, and *Taraxacum officinale*. The naturalized flora grew as species for food, forage, seasonings, and medicine were imported, cultivated, and escaped the bounds of cultivated fields. Importation of what has become the most common category of naturalized species, erstwhile ornamentals, had a modest beginning by the mid 17th century. The first recorded invasion, the spread and proliferation of *Linaria vulgaris* in the Mid-Atlantic colonies, was recognized by the mid 18th century, and *Berberis vulgaris* was rampant in southern New England before 1800. Botanical records, including published floras, became much more common in the first decades of the 19th century and reveal a naturalized flora in the U.S. that was quite similar in composition to the agricultural weed flora of Western Europe. Many ruderals and agricultural weeds were widespread in the eastern U.S., but probably not invasive by 1860, and included *Bromus secalinus*, *Cynoglossum officinale*, *Galium aparine*, and *Senecio vulgaris*. Other alien species had, however, become invasive by the 1840s, such as *Echium vulgare* in Virginia. Species that were to form devastating invasions in the United States from 1860 onward (e.g., *Bromus tectorum*, *Euphorbia esula*, *Lonicera japonica*, *Melaleuca quinquenervia*) had either not arrived by 1860, were undetected, or were not reported as having escaped from cultivation. Growth of the naturalized flora and the subsequent number of invasive taxa was certainly facilitated, and probably sparked, by the enormous growth of railroads and rail-borne commerce in the late 19th century.

Key words: *Berberis vulgaris*, biological invasion, John Bartram, *Echium vulgare*, *Linaria vulgaris*, naturalization, ornamental plants.

“... Behold, I have given you every herb bearing seed, which is upon the face of all the earth and every tree, in the which is the fruit of a tree yielding seed; to you it shall be for meat.”

—Genesis 1: 29. Bible, King James version

The first European human immigrants to North America had special reason to believe fervently in these words of Scripture. In transporting their families to a New World about which they knew little, they needed to believe that a Higher Authority would provide for their welfare. Most also firmly believed that God provided through the deliberate planning and industry of the faithful. Each band of European colonists to North America, whether the 16th century Spanish or Portuguese colonists (Crosby, 1972), 17th century English colonists to Maryland (Hall, 1910: 92), or the Pilgrims to New England (Young, 1846: 42), did not trust their survival to the happenstance acquisition of food in the New

World. From the outset, each group transferred crops and domesticated animals upon which they based their resolve to establish European agriculture in the New World (Mack, 2001, and references therein).

These determined attempts by European colonists and their American descendants to introduce non-indigenous plants in what was to become the United States have had profound and lasting influence on the floristic composition of North America's natural communities, and have largely determined which species have proved troublesome in agriculture, forests, rangelands, and inland waterways and lakes (Westbrooks, 1998). The size of the current naturalized, i.e., permanent non-indigenous, flora of the U.S. is not known precisely but exceeds 2500 species (Kartesz & Meacham, 1999). Of these, a small minority have become invasive, i.e., prolific and occupying significant new (i.e., non-native)

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ranges. These species, along with many other naturalized species, have caused enormous environmental and economic damage that ranges from threatening native biodiversity to changing the operation of major ecosystems (Mack et al., 2000; Pimentel et al., 2000).

European settlements in North America arose from fledgling colonies of immigrants that stemmed from different countries in western Europe and were established at different times and at widely spaced locales (Quinn, 1990). This mixture of circumstances and events suggests that the current naturalized flora has had a diverse origin and varied circumstances surrounding its eventual persistence. This diversity spawns a series of questions. What has been the chronology of plant naturalizations? More importantly, what can be deduced from that chronology about the circumstances that led some species to become naturalized early in the Europeans' history in North America, while other species became established much later? Which species, if any, formed pre-1860 invasions, and what sparked the demographic transitions among those few naturalized species that became invasive (Crooks & Soule, 1999; Kowarik, 1995)? What role have species introduced long ago into the U.S. continued to play in their new ranges? For instance, have they been supplanted by more recently arriving immigrants (Mack, 1989)? I chose to examine these issues for the period between 1634, the first records I am aware of for plant naturalizations, and 1860, before onset of the American Civil War and the enormous changes in the economy and transportation that so affected the U.S. for the rest of the 19th century and beyond (Kuznets et al., 1960; Meinig, 1986). These questions about plant entry, establishment, and their potential proliferation in new ranges must be considered because species' past immigration histories form part of the information upon which the prediction of future invasions will continue to rely (National Research Council, 2002).

METHODS

Any assessment of species that became naturalized long ago is intrinsically retrospective, and the record is incomplete and often fragmentary. Four general sources that vary substantially in potential accuracy and detail can be used in assembling this record.

- (1) Herbarium specimens provide unequivocal evidence for accurate species identifications. Consequently, they may form the best category of evidence, provided the collection

dates and locales are accurate. Unfortunately, the number of existing herbarium specimens across the time period under consideration here is meager. Few pre-1860 U.S. specimens still exist; even fewer have survived from pre-1800. Their use remains an unfulfilled goal here.

- (2) Pollen records can provide some supplemental information (Brugam, 1978) but are limited in their usefulness because many pollen taxa are impossible to identify with light microscopy and for some families, such as Poaceae, only a few genera are possible to identify in this way (Moore et al., 1991).
- (3) Contemporary regional floras became much more common after 1800, e.g., Pursh (1814) and Torrey (1819), and can be enormously informative.
- (4) The most common tool examined here consists of contemporary records and correspondence of those who provided first-hand accounts of the species they saw, their ranges, and abundances (e.g., Josselyn, 1672; de Schweinitz, 1832; Dwight, [1821] 1969; Gray, 1842).

Herbarium specimens, floras, and other records vary substantially in accuracy and scope, and until the later part of the 18th century, almost all employed only common names. I have cross-checked the common names (e.g., Fernald, [1950] 1987; Kartesz & Meacham, 1999) and avoided a species citation unless I could be confident of the identification. I have been similarly conservative in assigning an areal extent to any non-indigenous species. Fortunately, the same common names have been used consistently for many European ruderals and medicinal plants for more than 400 years, e.g., elecampane (*Inula helenium* L.), henbane (*Hyoscyamus niger* L.), horehound (*Marrubium vulgare* L.), and St. John's wort (*Hypericum perforatum* L.) (Harvey, 1974). In addition, a surprisingly high percentage (> 75%) of the species encountered in these early records were first described by Linnaeus, and many of these names have been retained in plant systematics. Given the limitations in the information that can be reliably deciphered about pre-1860 naturalizations, the resulting record will, however, remain a minimum estimate of the full scope of plant entry and establishment. Kartesz and Meacham's (1999) *Synthesis* was employed as the nomenclatural standard for plant names and authorities.

FIRST PLANT ARRIVALS: PRE-1700

Preparations for colonization of new lands in North America illustrate the care and forethought

that the immigrants placed in the undertaking. Isolated on a continent newly discovered by Europeans, connected to Europe only by infrequent and highly unreliable ship traffic, each colony's planners knew that they needed to become self-sufficient almost from the outset. Acquiring sustained sources of food and medicine figured foremost in their planning (Leighton, 1970). The most reliable early information we have of plans for colonizing North America stems from the establishment of Plymouth Colony, beginning in 1620. Although we do not know which species were in the original manifest, several lists of plants ordered in Britain from 1628 and 1631 have survived. The Endicott expedition in 1628 was to include "Wheat, rye, barley, oats, a hoghead of each in the ear, beans, pease, stones of all sorts of fruits, as peaches, plumes, filberts, cherries, pear, apple, quince, kernels, pomegranates, woad seed, saffron heads, liquorice seed, (roots sent and madder roots,) potatoes, hop roots, hemp seed, flax seeds against winter, coneyes, currants plants . . ." (Young, 1846: 42–43).

This intent to send woad seed (*Isatis tinctoria* L.), hemp seed (*Cannabis sativa* L.), and flax seed (*Linum usitatissimum* L.) forms the earliest record we have of the introduction of non-indigenous species that remain in the naturalized or at least the adventive flora of the U.S. Dyer's woad, *Isatis tinctoria*, has not apparently become widely naturalized in New England, despite its exceptionally early arrival (Magee & Ahles, 1999: 552), but it has become invasive in Utah and other arid regions (Farah et al., 1988). *Cannabis sativa* is widely naturalized in the eastern half of the U.S. north of the 37° latitude (Haney & Bazzaz, 1970). In contrast, flax appears commonly as an adventive in abandoned fields but may be naturalized only locally.

In 1631, just three years after the Endicott Expedition, John Winthrop, Jr., bought a detailed group of seeds from a London grocer with the intent of transporting these seeds to the small colony at Plymouth. Winthrop's (Massachusetts Historical Society, 1943: 47–48) list also included species that have since become naturalized, including "Sorrell" (*Rumex crispus* L. or *Rumex acetosella* L., or both), "Tansy" (*Tanacetum vulgare* L.), "Rockett" (*Eruca vesicaria* subsp. *sativa* (P. Mill.) Thellung [*Eruca sativa*]), "Buglos" (e.g., *Anchusa arvensis* (L.) Bieb.), "fennell" (*Foeniculum vulgare* P. Mill.), "dill" (*Anethum graveolens* L.), "sweet maioram" (*Origanum majorana* L. or *Origanum vulgare* L.), and "nipp" (*Nepeta cataria* L.), or adventives, such as "summer sauory" (*Satureja hortensis* L.), "Clary" (*Salvia sclarea* L.), "hysopp" (*Hyssopus officinalis*

L.), "marigold" (*Calendula officinalis* L.) and "hollihocks" (*Althaea rosea* L.) (Fernald, [1950] 1987; Magee & Ahles, 1999). The identification of other species on his list is more equivocal, such as "mallow," which may have referred to *Malva moschata* L., *Malva neglecta* Wallr., *Malva verticillata* L., or *Malva parviflora* L. The listing of "popey" (Massachusetts Historical Society, 1943: 47) may refer to *Papaver somniferum* L., the opium poppy, but could also be referring to *Papaver rhoeas* L., which had reputed medicinal properties. Winthrop's list also includes "pursland" or purslane (*Portulaca oleracea* L.). It is often considered non-indigenous to North America (Magee & Ahles, 1999), but appears in the fossil pollen and seed record of Ontario in pre-Columbian levels (Byrne & McAndrews, 1975). Although these species appear to have arrived with the first waves of colonists in New England, the earliest date when they became naturalized or even adventive is not known.

Our most comprehensive picture of the species introduced by 17th century colonists in New England is derived from Josselyn's 1672 publication *New-England's Rarities Discovered* and its 1674 sequel *An Account of Two Voyages to New-England*. Based on Josselyn's accounts of two visits, 1638–1639 and 1663–1671 (Josselyn, [1674] 1988: xiii), he appears to have been a keen observer of the condition of the colonies in New England. Furthermore, he deliberately categorized the species that he encountered in his travels between Massachusetts and Maine, noting those that were apparently native to New England, those species also found in England (and apparently introduced), and even those introduced species that did not thrive in their new locales. Among species that he reported that later became naturalized or at least adventive were many that are not among the manifests of Endicott or Winthrop. The naturalized species includecelandine (*Chelidonium majus* L.), goose-grass or "clivers" (*Galium aparine* L.), "Our English Clovergrass" (perhaps *Trifolium repens* L.), speedwell chickweed (*Veronica arvensis* L.), stitchwort (*Stellaria graminea* L.), St. John's wort (*Hypericum perforatum*), sweet brier or eglantine (*Rosa eglanteria* L.), toadflax (*Linaria vulgaris* P. Mill.), wormwood (*Artemisia absinthium* L.), and yarrow (*Achillea millefolium* L.). Among species now adventive are blueflowered pimpernel [*Anagallis arvensis* subsp. *foemina* (P. Mill.) Schinz & Thellung], "egrimony" (*Agrimonia eupatoria* L.), herb Robert (*Geranium robertianum* L.), "Oak of Hierusalem" (*Chenopodium botrys* L.), speed-well (*Veronica officinalis* L.), spurge time (*Polygonum persicaria* L.), "Rew" (*Ruta graveolens* L.), watercress (*Rorippa nastur-*

tium-aquaticum (L.) Hayek), and wild-mint (*Mentha aquatica* L.) (cf. Magee & Ahles, 1999). Furthermore, Josselyn (1672: 85) took the extraordinary step of noting which species had arrived "... since the English Planted and kept Cattle in New-England" that were already occurring spontaneously without cultivation. In this list, Josselyn provided explicit information on some of the first naturalized species (see below).

The diversity of species in Josselyn's list reveals that by 1671 (his last year in North America), and perhaps much earlier, the small lists of species that Endicott and Winthrop had ordered for the settlers had been expanded severalfold. Most prominent are species that had reputed medicinal value (*Artemisia absinthium*, *Hypericum perforatum*, *Inula helenium*), as well as plants for seasonings (*Anethum graveolens*, *Foeniculum vulgare* P. Mill., *Salvia sclarea*). Perhaps most surprising is that the colonists were beginning to feel confident enough about their survival that they permitted themselves the luxury of importing a few ornamental species, *Linaria vulgaris* and *Rosa eglanteria* (Leighton, 1970). Both of these species would become naturalized, and *L. vulgaris* would become a scourge by the mid 18th century. The arrival of these species is also significant because this early entry of ornamental species signals a trend that would grow substantially over the following 350 years as ornamental species became the largest single functional category of imported species (Mack & Erneberg, 2002).

EMERGENCE OF THE FIRST NATURALIZED SPECIES: PRE-1700

Our ability to detect the earliest naturalizations is severely limited by the fragmentary character of the first accounts of European colonists in North America. For example, the late 16th century Spanish settlements in Florida included gardens and cultivated limes, lemons, and oranges (Lyon, 1996: 55); contemporaneous introductions of oranges soon appear in other Spanish subtropical and even temperate colonies (Gade, 1976). I am, however, unaware of any information on the fate of these species that were cultivated in 16th century Florida. Maine also received European colonists very early: successive temporary settlements were made beginning in 1604. The record referred to as the Edgerton Manuscripts (Lockwood, 1931: 139) is intriguing in describing the author's visit to a long-abandoned settlement in Maine "on the Permaquid River Alderman Alsworth of Bristole settled a co., of people in 1625. . . . In 1675 I found the Roots and Garden Herbes, and some old walls

there when I went first over, which showed it to be the place where they had been." Finding garden herbs many years after the site's abandonment strongly suggests that these species had become naturalized.

The first, admittedly tenuous, records of naturalized species in what was to become the U.S. appear in the decades after establishment of English colonies in New England. Among the praiseworthy features of these English immigrants was their commitment to recording a wide range of information about their nascent settlements, including the fate of their crops. Only 14 years after the first colonists landed in Plymouth Bay, William Wood (Wood, [1634] 1977) had published his account of the "New England's Prospect": a comprehensive report of information that would have proven invaluable to anyone intending to immigrate to New England. Wood's comments entitled "Of the Herbes, Fruites, Woods, Waters and Minerals" prove particularly informative about both the European crops being planted and also those already observed to persist outside cultivation.

Wood's ([1634] 1977: 36) listing of the crops, both native and introduced, reveals species that had already been brought under cultivation and their status: "The ground, affords very good kitchen Gardens, for turneps, Parsnips, Carrots, Radishes, and Pumpkins, Muskmillions, Isquoutersqashes, Coucumbers, Onyons, and whatever grows well in England grows well there, many things being better and larger; there is likewise all manner of Herbes for meate, and medicine, and that not only in planted gardens, *but in the Woods, without eyther the art or the help of man, as sweet Marjoram, Purselane, Sorrel, Peneral, Yarrow, Mirtle, Saxifarilla, Bayes, etc.*" (italics added). The italicized statement strongly suggests that several of the species that the colonists had planted in the previous decade had already escaped cultivation and were growing freely in the surrounding forest. These species include sorrel (*Rumex acetosa* L. and *Rumex crispus*) and yarrow (*Achillea millefolium*). These are the earliest accounts I am aware of for any naturalizations in North America. Identification of "sweet Marjoram" is equivocal. Wood may have been referring to *Origanum majorana*, which is still referred to as sweet marjoram, but has rarely escaped cultivation and is not considered naturalized in New England today (Magee & Ahles, 1999: 898). Alternatively, he may have seen *Origanum vulgare*, now termed wild marjoram, which is naturalized (Magee & Ahles, 1999: 873). "Peneral" in Wood's list may refer to the native species *Hedeoma pulegioides* (L.) Pers. rather than the European species, *Mentha pulegium*

L., for which there is no record of naturalization in the U.S.

These earliest references to the naturalized status of some newly arrived European species in New England are substantially corroborated and expanded by Josselyn (1672). His list "Of such Plants as have sprung up since the English Planted and kept Cattle in New-England" is the best account from which to determine the European species that had become naturalized by 1671 and probably much earlier (Josselyn, 1672). Many of the species that he reported in terms indicating their newfound persistence in the New England flora are still prominent today (Magee & Ahles, 1999), such as *Hyo-scyamus niger*, *Stellaria media* (L.) Vill., *Taraxacum officinale* G. H. Webber ex Wiggers, *Senecio vulgaris* L., and *Urtica dioica* L. Josselyn's (1672: 86) report that plantain (*Plantago major* L.) was referred to by Native Americans as "English-Man's foot" has been quoted repeatedly. Plantain was already spreading along paths and roads well ahead of English settlements and served as a harbinger to the aborigines of the coming of the new settlers (Darlington, 1859: 219).

Aside from the immediate needs for importing plants for food and medicine, the early colonists had definite interest in ensuring that their livestock had suitable forage. They soon found, however, that the coastal environments offered their animals little nutritious forage. A common complaint is exemplified by one colonist in Massachusetts who stated that his livestock "... grew lousy with feeding upon it, and are much out of heart and likeing ... " (Hutchinson, [1764] 1972: 483). Help was on the way. These transplanted English farmers and herdsmen were well acquainted with an array of "English grass" that would meet their livestock's needs, and they actively sought seeds of these English pasture species for introduction into their farms. Species identifications in these 17th century accounts are confounded by the common reference to a mixture of grasses and clovers as "English grass," and it is likely that some of these species could have arrived alternatively as seed contaminants in lots of seed or in the ballast or debris off-loaded from ships with livestock, or both (Bidwell & Falconer, 1925). Species that were introduced through the 17th century were *Polygonum aviculare* L., *Holcus mollis* L., *Poa pratensis* L., and possibly *Agrostis capillaris* L. (Carrier, 1923: 241), and *Holcus lanatus*. Not only were these species becoming naturalized in New England, but they were also being actively spread in colonies to the south. In praising the growth of cattle and other livestock on Long Island (New York), Denton (1670: 5) commented that "the Is-

land likewise [was] producing excellent English grass, the feed of which was brought out of England, which they sometime mow twice a year." And Budd (1685: 10) commented on the practice of using sheep to disperse these grasses "but if we sprinkle a little English grass Hay-Seed on the Land without Plowing, and then feed Sheep on it, in a little time it will so increase, that it will cover the Land with English Grass, like unto our Pastures in England. . . ."

Naturalizations arising from the introduction of forage species were not restricted to grasses. The advantages of sowing pastures with clovers, especially *Trifolium repens* (white clover), were common knowledge in England by the mid 17th century, and this knowledge was widely transferred to North America. As early as 1635 a tract written for those who planned to immigrate to Maryland advised that they bring "Good store of claver grasse seede, to make good meadow" (Hall, 1910: 98). This sound advice had also been followed in New England: Josselyn ([1674] 1988: 131) commented that "Our English clover grass sown thrives very well." It was both deliberately sown and spread as sheep were moved among fields, as Scot (1685: 187–188) recorded for New Jersey: "As soon as any of the land here comes to be cultivated, it over-runs with small Claver-grass, by the pasturage and dunging of the cattle, and so supplants the naturall grass and hearbs." The movement of livestock and seed among the colonies was extending the new ranges for these European pasture species.

By the mid to late 17th century at least 20 species were observed to have already become naturalized in New England; many of these had likely become established further south in Pennsylvania. The actual number of naturalized species was likely much larger. For example, Josselyn (1672) listed under his category "Of such Plants as are common with us in England" many species that were already in New England and for which we have records of naturalization in the 18th century. How long before 1700 they were naturalized we do not know. Species in this category of 17th century introductions that were to become permanent residents include *Artemisia absinthium*, *Cannabis sativa*, *Galium aparine*, *Hypericum perforatum*, *Inula helenium*, *Nepeta cataria*, and *Xanthium strumarium* L.

PLANT ARRIVALS AND NATURALIZATIONS IN THE 18TH CENTURY

Any chronological divisions, such as those between centuries, that could be used to delineate the growth of a naturalized flora are arbitrary. The forc-

es that brought new species to North America and contributed to their naturalization were obviously not so coincidentally partitioned as to conform to even decadal, much less centennial breaks. Nevertheless, there is some justification for distinguishing between the naturalizations in the 17th and the 18th centuries. Leighton (1976: 1) has argued that the necessity of establishing self-sufficient colonies in the 17th century was a powerful incentive to ensure that almost all the species introduced before 1700 were for utilitarian purposes. As noted above, some plants introduced even before 1650 may have had no purpose other than ornamentation, such as *R. eglanteria*. But even *R. eglanteria* may have been deliberately introduced to form hedges (Joselyn, 1672: 90). In contrast, the assurance that the colonies would not only survive but also grow and prosper sparked much incentive in the 18th century for the introduction of species for the widest range of uses, especially for ornamentation. This market in ornamental species grew steadily throughout the 18th century and thereby created opportunity for more naturalizations, and even invasions (Lockwood, 1931: 12; Leighton, 1976).

Perhaps the best single view we have of the growth of this naturalized flora in the 18th century was a retrospective written in the early part of the 19th century but clearly drawn from information gathered in the late 18th century. Rafinesque, an itinerant French botanist, collected plants widely in the new United States. In 1810 he assessed the naturalized flora of the Middle Atlantic states (Rafinesque, 1811). His work appears to be based largely on Muhlenberg's (1793) flora of the area surrounding Lancaster, Pennsylvania, *Index Florae Lancastriensis*, which Rafinesque augmented and annotated to include his own observations for the North American region that stretched south from New York State to Maryland. The most specific location information is given for species occurring near Lancaster, Pennsylvania, and those found in the vicinity of Baltimore, Maryland, Rafinesque's home in the U.S.

In a useful pattern that was to be repeated by other authors in the 19th century, Rafinesque (1811) categorized the species on their mode of introduction: plants introduced by agriculture, plants introduced by gardening, and "totally useless" plants or weeds, i.e., those accidentally introduced. Plants in a fourth category for him had varied modes of introductions and were not native to Europe. A great advantage of this Muhlenberg *cum* Rafinesque list is the consistent use of binomial names, most of which have been retained in modern plant systematics. In addition, Rafinesque gave his

assessment of the abundance of the species, making it clear that a few (*Convolvulus arvensis* L., *Leucanthemum vulgare* Lam. [which he termed *Chrysanthemum leucanthemum*], and *Verbascum blattaria* L.) were both widespread and abundant. Among deliberately introduced species are *Cannabis sativa*, *Hordeum vulgare* L., *Linum usitatissimum*, *Plantago lanceolata* L., and *Trifolium pratense* L., which were all listed as common to very common, usually in ruderal sites.

Of the more than 300 species in Rafinesque's (1811) list, he considered the largest single group (193 taxa) to have been introduced in gardening, i.e., species grown in small plots and presumably cultivated much more assiduously than field crops (e.g., *Glechoma hederacea* L., *Sinapis alba* L.). The second category reveals the extensive naturalization of medicinal plants and those used for seasonings in the 18th century: *Asparagus officinalis* L., *Cynoglossum officinale* L., *Digitalis purpurea* L., *Inula helenium*, *Marrubium vulgare*, *Nepeta cataria*, and *Tragopogon porrifolius* L. Most of these species were listed as common and confined to roads, near dwellings and gardens. Among this large list of species are also those such as *Cichorium intybus* L. (chicory), which was listed as "very common—in fields, roads, cultivated grounds. . .," and *Lamium amplexicaule* L., considered, "every where common—in fields."

Many more species had been imported for strictly aesthetic reasons in the 18th compared with the 17th century, and among these were some that soon became naturalized. Ornamental species that had already become naturalized ca. 1800 in Rafinesque's opinion included *Euonymus europaea* L., *Ligustrum vulgare* L., *Rhamnus cathartica* L., and *Syringa vulgaris* L., illustrating that woody ornamental species were also becoming persistent. The remainder of the species noted by Rafinesque were considered accidentally introduced, such as *Bromus secalinus* L., *Echium vulgare* L., which was to become much more conspicuous later, *Agrostemma githago* L., *Chenopodium album* L., *Convolvulus arvensis*, and *Spergula arvensis* L.

Rafinesque (1811) may have applied the appellation "naturalized" rather liberally, as he used it to mean those species that ". . . now grow spontaneously . . .," not necessarily persistently. For example, he listed some species, such as *Fagopyrum esculentum* Moench (buckwheat), as naturalized and common, yet today it is probably only adventive as an escape from cultivated fields. Alternatively, its status may have indeed changed in the last 200 years (e.g., from diminished cultivation), or he may have been simply noticing volunteer

buckwheat that was residual in fields. Another species he considered rare but nonetheless naturalized was *Rubia tinctoria* L. (madder), a species referred to among some of the earliest plant import manifests in the 17th century (Young, 1846: 42) but which is considered as only a rare escape from cultivation today (Magee & Ahles, 1999). Nevertheless, the bulk of the species that he noted as naturalized are indeed persistent today, and his assessments were corroborated by his contemporaries.

EMERGENCE OF THE FIRST PLANT INVASIONS: 18TH CENTURY

The major consequences of non-indigenous species result from the small minority of naturalized species that become prolific in the new range, i.e., these species become invaders. Their abundance and aggressive growth bring about environmental damage to the native species and alteration of native environments (Mack et al., 2000). These species often invade arable fields and pastures and consequently result in severe economic damage (Bridges, 1992). Given the growing array of non-indigenous species that were being introduced both accidentally and deliberately from the early 17th century onward, it is not surprising that a few were eventually reported in terms that we would equate with plant invaders.

The earliest invasion of which I am aware resulted from the introduction of *Linaria vulgaris* P. Mill (yellow toadflax). In the extensive correspondence that John Bartram, the doyen of 18th century American botany, maintained with his colleagues Peter Collinson and Philip Miller in Britain (see Darlington, [1849] 1967), his remarks about *L. vulgaris* are revealing. In a report that both colleagues apparently received accompanying a letter in 1758, Bartram stated, "It was first introduced as a fine garden flower; but it was never more heartily cursed by those that suffer by its encroachment" (Darlington, [1849] 1967: 384). He added, "It is the most hurtful plant to our pastures that can grow in our northern climate. Neither the spade, plough, nor hoe, can eradicate it, when it is spread in a pasture" (Darlington, [1849] 1967: 383). Bartram explained that so desperate were farmers to control yellow toadflax that they would even ignite log piles in a field in the hopes of destroying it in the soil but to no avail. Bartram reported that by 1758 *L. vulgaris* had "... spread over great part (sic) of the inhabited parts of Pennsylvania" (Darlington, [1849] 1967: 384)—a clear indication that it was not simply a local problem. *Linaria vulgaris* had

formed an invasion. It apparently spread further afield: Pursh (1814) noted that it had become "... one of the worst and most troublesome weeds in several parts of Pennsylvania and Virginia." Barton (1818) went even further in his estimation of its spread as he rated it (which he termed as *Antirrhinum linaria*) as "... extensively naturalized, in the United States. On roadsides, commons, wastes, and the borders of fields, very common and abundant." Yellow toadflax had reached North Carolina by 1832 because de Schweinitz (1832) reported that a few years after *L. vulgaris* (as *Antirrhinum linaria*) was introduced into a garden it had "... contaminated the whole vicinity for many miles."

Other naturalized species were also causing serious problems, although the extent of their new ranges is more difficult to determine. Bartram lived in Philadelphia but had numerous correspondents along the East Coast, so some of his assessments of the damage from naturalized species may have been drawn in part from the reports of others. For example, Bartram in the same 1758 correspondence listed other non-indigenous species in what appears to be a declining order of prominence. He described *Hypericum perforatum* as a "very pernicious weed," which had spread over pastures in eastern Pennsylvania, interfering with the growth of pasture grasses and causing injury to horses and sheep (Darlington, [1849] 1967: 384). This plant was apparently introduced repeatedly in New England and the Middle Atlantic colonies (Josselyn, 1672: 44; Haughton, 1978: 348), so it may well have formed an invasion by the mid 17th century. *Hypericum perforatum* was also proving to be a troublesome plant in fields in New England. Eliot, writing in his fourth essay on agriculture, which was first published in 1753, complained about the difficulty of eliminating St. John's wort in fields (Carman & Tugwell, 1934: 94). Even though Eliot lived in Connecticut, he traveled widely in New England, and his essays were meant to be advice gleaned from decades of observation in the region (Carman & Tugwell, 1934). If *H. perforatum* had not reached the status of an invasion by the mid 18th century, it was at least a widely distributed naturalized species.

Linaria vulgaris and *Hypericum perforatum* bedeviled 18th century farmers across a broad region from Pennsylvania to New England, but these species' prominence appears to have since declined. Darlington (1859: 225) reported that *L. vulgaris* was "extensively naturalized" and a "vile nuisance in our pastures and upland meadows." He described *H. perforatum* as a "rather troublesome weed on our farms," but did not state it in terms that suggest an

invasion. He added the intriguing note that in Chester County, Pennsylvania, he noticed that the plant was not detected at all in 1842, and was rare in 1843, but had become “as common as ever” in subsequent years (Darlington, 1859: 55). This statement may allude to the prominence reported by Bartram in the 18th century (Carman & Tugman, 1934).

Although widely naturalized in the northeastern U.S. (Rhoads & Klein, 1993; Magee & Ahles, 1999), neither *H. perforatum* nor *L. vulgaris* appears invasive today. However, these reduced roles are largely the result of active control measures. *Linaria vulgaris* is controlled with the herbicide glyphosate in agricultural fields (Saner et al., 1995), while the abundance of *H. perforatum* has been effectively curbed in much of its new range through biological control (Julien & Griffiths, 1998, and references therein). The difficulty in deciphering from early accounts whether species had become invasive relates to the specific interests of the observer. Eliot and Darlington were primarily interested in species that were hazards to agriculture. Even Bartram’s observations appear often influenced by his concern about agriculture. Alien plants that were extensive exclusively in non-agricultural settings may not have been commented on.

As damaging as *L. vulgaris* and *H. perforatum* could be, colonial farmers already had a much greater scourge to cope with—*Berberis vulgaris* L. (common barberry), the alternate host for the stem rust (*Puccinia graminis* f. sp. *tritici*), a devastating parasite of cereal crops (Peterson, 2001). *Berberis vulgaris* had certainly reached the level of impact to qualify as an invader by the late 18th century and had probably reached that status over a century earlier. Our knowledge of its probable entry into North America by the mid 17th century is through a combination of its direct mention and reports of the occurrence and spread of stem rust as it infected wheat across New England. Common barberry was almost certainly introduced deliberately in the 17th century, as it was valued in sauces and as a medicinal plant (Gerard, [1633] 1975: 1326). Josselyn (1672) referred to “barberry trees” in a list of introduced fruit trees and also described the rust (termed “wheat blast” until the 20th century) on wheat in New England in the 1660s. A more detailed account of the incidence of stem rust was provided by John Winthrop in 1668: “generally through all the plantations, both of ye Massacheussetts colony, Plymouth, & this also [the colony of Connecticut] insomuch that the croppe of wheat hath failed divers yeares in most plantations. The corne flourished well till it came to be eared, and

the eares also would appeare faire, and as if full, but no corne in them. There have beene thousands of acres in that maner every yeare. What the cause was, whether naturall, or a blasting fro heaven we know not. Our old husbandmen of England, some of them thought it a mellow . . .” (Bidwell & Falconer, 1925: 13). Given the obligate link between wheat, stem rust, and barberry, it seems a safe inference that where rust was attacking wheat, barberry was nearby.

As further evidence for the spread and impact of *Berberis vulgaris*, Connecticut passed legislation in 1726 to control barberry, followed by Massachusetts and Rhode Island in 1755 and 1772, respectively (Fulling, 1943). These measures failed, as Dwight ([1821] 1969) provided direct observation in 1795 or 1796 of the extent of *B. vulgaris* across much of eastern Massachusetts and coastal New Hampshire. Within the approximately 3000 km² area that Dwight circumscribed in his travels he noted “. . . the barberry bush is spread, not universally, but in spots, and those often extensive. In some fields they occupy a sixth, fifth, and even a fourth of the surface” (Dwight, [1821] 1969: 276). Clearly, barberry was exerting a major influence on wheat production across eastern Massachusetts in the 18th century to the point that bread made from wheat had disappeared from farmers’ diets in much of New England (Bidwell & Falconer, 1925: 92). Common barberry would later spread much further across the U.S., and by the time control efforts were fully implemented against it early in the 20th century, it was extensive in a 13-state area in the North Central region of the U.S. (Hutton, 1927).

Other biotic invasions were growing in North America by the late 18th century, e.g., the spread of *Trifolium repens*, even if the proliferation of an alien clover does not produce the usual anthropocentric connotations. As stated previously, *T. repens* had been spread both deliberately and accidentally through New England and colonies, such as Pennsylvania and New Jersey, in the 17th century. The resulting transformation of pastures, for which it was valued, represents substantial increases in the soil nitrogen pool in these sites. Such change can precipitate a host of other environmental changes, including a facilitation in the establishment of other alien species. For example, introduction of the nitrogen-fixing Firetree, *Morella faya* (Ait.) Wilbur, so raised the amount of biologically available nitrogen in Hawaiian soils that Firetree has favored the persistence of other non-indigenous species (Vitousek et al., 1996).

GROWTH OF A NEW NATION'S NATURALIZED
FLORA: 1800–1860

All the incentives and stimuli that had operated before 1800 for the introduction of non-indigenous plants expanded substantially with the growth of the new nation's commerce and transportation in the 60 years leading up to the Civil War in 1861 (Meyer, 1917). New species were actively sought out that would contribute to the national economy, and for the first time these searches were not left simply to private enterprise. In an often-quoted proclamation, President John Quincy Adams in 1827 instructed U.S. consular offices to gather useful species and U.S. naval ship captains to provide for the transport of these living cargoes to the U.S. (Hodge & Erlanson, 1956). Annual reports of the Commissioner of Patents, who was responsible for federal involvement in agriculture before 1863, routinely chronicled federal interest in introducing new species in the U.S. for potential use (e.g., U.S. 28th Congress 1st Session, 1844: 68; U.S. 36th Congress, 2nd Session, Ex. Doc. 48, 1861).

Federal actions were dwarfed, however, by the private sector's economic incentive to import species new to the U.S. for all manner of use, particularly as ornamentals. Establishment of commercial nurseries and seedsmen in major cities, particularly Philadelphia, even before the American Revolution (Lockwood, 1931: 12), was followed by a huge growth in this cottage industry through the first half of the 19th century (Leighton, 1987: 67; Mack, 1991, and references therein). These seedsmen were remarkably diligent, not only acquiring new species from overseas but also in building clientele that were not restricted to the immediate vicinity of their businesses and gardens. By 1804 Bernard M'Mahon, a Philadelphia seed merchant, was advertising that he had within his nursery collection species from such far-flung locales as the "South-Sea Islands," Asia, Africa, and Europe (M'Mahon, 1804). The product of such industry was the availability of several hundred species for sale that had not before entered the U.S. (Leighton, 1987; Mack, 1991). Many of these species were to become naturalized by 1900, such as *Casuarina equisetifolia* L., *Cyperus esculentus* L., *Hedychium gardnerianum* Shepard ex Ker-Gawl., *Lonicera japonica* Thunb., *Lysimachia nummularia* L., *Morella faya*, *Tamarix* spp., and *Ulex europaeus* L. (Mack, 1991).

Occasionally, single events are recorded that may have spawned a naturalization. *Cytisus scoparius* (L.) Link, Scotch broom, is a notorious sprawling shrub that rapidly covers new range through a

combination of vegetative propagation and local seed dispersal from explosive capsules. Once it occupies a site, it can form an impenetrable thicket that reduces the prevalence of other plants and interferes with the movement of livestock (Peterson & Prasad, 1998). Although there are apocryphal reports of earlier introductions (Lockwood, 1934: 32), the earliest clear reference to the shrub in Virginia arises in a letter (Anonymous, 1921) detailing the misguided generosity of J. M. Galt, a visitor to the farm of John Cocke in Mount Pleasant, Virginia, in 1803. Learning that Cocke intended to introduce an unidentified species to his farm as sheep fodder, Galt wrote with news about what he deemed a superior choice: "When I was at your house you mentioned your Intention of Cultivating the Pride of China for feeding sheep. This will answer for the winter months very well. It did not occur to me then to recommend to your notice the cultivation of Scotch Broom, which affords an ample food for between two or three summer months for sheep and hogs. . . ." Dr. Galt gave more than advice; he also sent along seeds of *C. scoparius*: "I have sent you seed sufficient to plant all your hill sides that you do not mean to cultivate in grain." The seeds had been imported by Galt from a farm in Warwick, England, a few years earlier. His account of the plant's behavior on the Warwick farm seems particularly ominous in retrospect ". . . it was originally planted as a hedge by an old Englishman—from which it has spread over some hundreds of acres of land by the Birds." To ensure that the spread of Scotch Broom would be complete, Dr. Galt helpfully added the following tip: "in England they have a method of Expediting Vegetation of Broom—Hawthorn and Holl—by mixing the seeds with the feed of their horn'd Cattle & keeping the Cattle up until they have passed the seed—they then sprinkle this over their Land & plough it in, in the fall season, in the spring the seed will vegetate . . ." (Anonymous, 1921). Unknown is whether the land owner, John Cocke, actually sowed the seeds given by Galt. However, *C. scoparius* remains naturalized in Virginia in scattered locales (Harvill et al., 1992).

Records of the escapes and naturalizations of these new immigrant species, as well as confirmation of the naturalized status of many other species imported much earlier, are established through the proliferation of published local and regional floras along much of the East Coast of the U.S. and even at newly established inland settlements (Sullivant, 1840). Pursh (1814) and Torrey (1824) exemplified ambitious early attempts to record floras that were not confined to urban seaports. Their records are

invaluable because these early U.S. botanists confidently assigned Latin binomials to their collections and often reported in unambiguous terms whether these species were naturalized. Thus, Pursh (1814) was able to describe the noxious alien grass *Eleusine indica* (L.) Gaertn. as occurring in sandy soil from New Jersey to Florida, *Festuca elatior* [probably *Lolium pratense* (Huds.) S. J. Darbyshire] as occurring in wet meadows in Pennsylvania and New England, and *Urtica dioica* as found from Canada to the Carolinas. Even if the geographic range was restricted, the notes on the status of these species is nonetheless valuable, e.g., Barton's (1818) *Compendium florae philadelphicae*, which was restricted to sites within 10 miles of Philadelphia. For example, Barton (1818) described *Ranunculus bulbosus* L. as so abundant that "... whole fields are often rendered yellow by the profusion of the plant" and *Allium vineale* L. as common, pestiferous, and "... impossible to eradicate."

As valuable as published floras of the early 19th century are in tracing the earliest record and fate of non-indigenous species, authors such as Pursh, Torrey, and Barton were not concerned specifically with these species and their effect in the U.S. Coming approximately 30 years apart, the accounts of de Schweinitz (1832) and Darlington (1859) provide extraordinarily valuable benchmark accounts that deal explicitly with the scope and status of non-indigenous species along the East Coast of the U.S. Although the detail of their investigations and observations differ in geographic range, these two accounts provide perhaps the best guides we have on the growth of the naturalized flora across the first half of the 19th century.

De Schweinitz (1832) explicitly dealt with species that had become naturalized in the U.S., including a grouping of species by their mode of introduction: those introduced deliberately for cultivation and those ostensibly introduced as seed contaminants ("Introduced fortuitously with agricultural seeds") (de Schweinitz, 1832: 151). De Schweinitz provided a separate list of plants that he considered naturalized in smaller areas, e.g., individual states or urban areas. Furthermore, he provided an unambiguous definition for "naturalized" species: "... which are regularly reproduced, and gradually extending themselves, without present cultivation..." (de Schweinitz, 1832: 149). His list of deliberately introduced species included many that had been introduced at least a century earlier: *Anthoxanthum odoratum* L., *Nepeta cataria*, *Plantago major*, *Taxaracum officinale*, and *Verbascum thapsus* L. But this category also included apparent newcomers, such as *Barbarea vulgaris* Ait. f., *Poa*

annua L., and *Raphanus raphanistrum* L. His list of accidentally introduced species included *Allium vineale*, *Cerastium vulgatum* [probably *Cerastium fontanum* subsp. *vulgare* (Hartman) Greuter & Burdet], and *Lolium perenne* L. These species may have been introduced in the 18th century as there is no mention of them before 1700. Species that were naturalized locally, i.e., without the extensive new range occupation he observed for others, included *Anagallis arvensis* L., *Briza media* L., *Bromus hordeaceus* L., *Dactylis glomerata* L., and *Inula helenium*. Unfortunately, de Schweinitz did not describe these species in terms of their abundance and impact, especially in terms that would allow evaluation of any invasive role.

Darlington's (1859) *American Weeds and Useful Plants* provides probably the best overview we have of the composition and impact of the non-indigenous flora ca. 1860. Darlington was explicitly concerned with those species that were troublesome in agriculture; then as now most agricultural weeds are non-indigenous (Bridges, 1992). He recorded about 400 non-indigenous taxa that were established in the eastern third of the country, but it is clear that his collections and observations are drawn from the Middle Atlantic States, the collecting area of Rafinesque 50 years earlier. Darlington repeatedly referred to species as "naturalized" (e.g., *Sisymbrium officinale* (L.) Scop.), in contrast to other species that were merely present in the U.S. by the 1850s. For other species, it certainly appears that he also considered them as naturalized, e.g., in referring to the Scotch thistle *Onopordum acanthium* L. as "... very common along road-sides and in waste places in New England" (Darlington, 1859: 199). Interesting in this regard is his assessment of all *Galium* species, which he dismissed as "... not sufficiently important even as weeds to require notice" (Darlington, 1859: 164). He reported that the flax dodder *Cuscuta epilinum* Weihe had become quite rare because of the decline in the cultivation of *Linum usitatissimum*, its host. He also recognized that some species, such as *Ailanthus altissima* (P. Mill.) Swingle (tree-of-heaven), had both beneficial and detrimental qualities: providing urban shade but also escaping to vacant lots and even emerging from pavement.

PLANT INVASIONS BY THE MID 19TH CENTURY

An invasion is commonly dependent on the immigrant species being transported to many suitable localities in the new range (Moody & Mack, 1988). The disseminules of some species are readily carried by wind, water, or animals (Ridley, 1930) and

can rapidly fill a new range with little or no human assistance. But the spread of many others within a potential new range is greatly facilitated by human agencies. Consequently, as the network of roads, canals, and railroad routes grew in the 19th century U.S., the spread of non-indigenous species also expanded. Some of these routes or pathways were being developed even before 1800. For example, there was a comprehensive network of national postal roads that linked the country from north to south by 1804 (Paullin, 1932). Additional roads, supplemented by canals and established barge traffic along major rivers, such as the Hudson, the Ohio, and the Delaware, extended this network (Meyer, 1917). Even by the early 19th century, commerce, including seeds and seed-contaminated cargo, was moving routinely throughout the new nation.

The extent of the American commercial network, as well as the volume of goods moved in the interior of the country, increased markedly with the growth of railroad lines. The first U.S. railroad routes were built in the 1830s. New lines were added rapidly, and most importantly, these lines became linked, so that goods could be moved hundreds of miles in days, not the weeks or months that were needed even along the national trunk roads. From 1830 to 1850, the total length of the railroad system grew from 117 to more than 14,200 km in 27 states in the eastern half of the nation (Meyer, 1917: 573). Growth over the following ten years would dwarf even this total (Meyer, 1917, plate 5).

At least one plant invasion appears to have been added in the early 19th century to those that had begun earlier. Asa Gray, who was to become the doyen of American botany in the second half of the 19th century, was by his estimation the first botanist to explore the Shenandoah Valley (Gray, 1842). Upon reaching Winchester, Virginia, at the northern end of the valley in June 1841, he traveled south. Throughout the broad valley for over a hundred miles Gray was amazed to see immense amounts of *Echium vulgare* L. (viper's bugloss), a Eurasian biennial, occupying many sites, including cultivated fields. Arriving in late June Gray saw viper's bugloss in full flower and described how it formed a "... broad expanse of brilliant blue" (Gray, 1842: 13). Gray's account of the geographic spread and prominence of *E. vulgare* at this time leaves little doubt that he was describing an invasion. He was surprised that farmers had allowed the plant to overrun their fields. Their reluctance to remove it may have stemmed in part from the difficulty of handling it, as it causes contact dermatitis (Magee & Ahles, 1999). Gray (1842) further

reported that in the northern states he had seen it only as an occasional roadside plant. Darlington (1859: 242) later reported that he had seen it in "considerable quantities" in Maryland and in abundance in New York. Viper's bugloss may have been introduced deliberately among these widely separated sites because it was valued as a medicinal plant (Parsons & Cuthbertson, 1992: 332).

It is intriguing that this plant, which was so prominent in the mid 19th century in Virginia and elsewhere, would be viewed today as locally abundant but not invasive anywhere in the U.S. (Lorenzi & Jeffrey, 1987: 245). The abundance of a plant invader can decline precipitously, e.g., *Agrostemma githago* in Britain (Clement & Foster, 1994), through a change in agricultural practices. Given the need to control plant invasions, understanding the demise of invaders such as *E. vulgare* in Virginia becomes an important topic for experimentation. The ability to identify this species' pollen in 19th-century sediments could aid in this investigation (cf. McGlone & Basher, 1995).

The list of invasions under way by 1860 likely included more species than *Cytisus scoparius* and *Echium vulgare*, although the strength of evidence for the others is more circumstantial. Darlington (1859) was concerned primarily with the spread and damage of weedy species in agriculture and only incidentally with those species' occupation of other sites. Nevertheless, he did describe the range and impact of several dozen species in such terms that suggest these were invaders. In fact, he described *Aegopodium podagraria* L. (goutweed) as an invader that "... should be carefully watched and its spread arrested" (Darlington, 1859: 151). The strength of the descriptors he used for a few species is a guide to their impact. For example, Darlington (1859: 197) referred to *Cirsium arvense* (L.) Scop. as "... perhaps, the most execrable weed that has yet invaded the farms of our country." Similar language was applied to the spread and impact of *Cyperus rotundus* L. in its role on cultivated ground in the South, especially in sandy fields and sand drifts and along the seacoast. *Leucanthemum vulgare* Lam. (which he termed as *Chrysanthemum leucanthemum*) may have also reached the status of an invader because Darlington (1859: 189) described it not only as a "great nuisance in our country" but also as having "in some districts ... exclusive possession of their pasture fields." It is apparent in Darlington's description of the status of *Echium vulgare* and *Berberis vulgaris* that these two earlier recognized invaders had maintained their role until at least the mid 19th century.

Collectively these invasions had already sparked

attention and admonishments to farmers to apply diligence in keeping their fields free of these pests and to sow and trade crop seeds that were free of these damaging contaminants (Darlington, 1859: 242). Even if farmers had universally accepted the advice, it would have been difficult to carry it into practice. Threshing equipment in the early 19th century was a poor match against the seed mimics (e.g., *Avena fatua* L., *Bromus secalinus*) that contaminated crop seeds, and a great wave of new introductions were headed to the U.S. (Mack, 1991). As a result, many of the naturalized species that were to become ruderals in the U.S. were not only in the country by 1800, they had been spread throughout much of the eastern half of the U.S. by 1860. In contrast, many other species that have become invaders in the U.S. were just being detected by this date, such as *Bromus tectorum* L. (Bartlett et al., 2002) and *Lonicera japonica* (Schierenbeck et al., 1994) or had yet to be detected (e.g., *Salsola kali* L.). In a sense, the damage caused by plant invaders in the first 200 years or more of European colonization along the eastern coast of the United States would be far outweighed by the damage brought about by species introduced or deliberately spread post-1860.

CONCLUSIONS

Several timely observations can be gleaned from tracing the growth of the naturalized flora in the U.S. between the early 17th and mid 19th centuries. From the beginnings of European colonization in North America, the list of plants that became naturalized was shaped strongly by the species human immigrants selected for their transplanted agriculture. Even if a naturalized species did not owe its new status to deliberate introduction, it likely arrived as a contaminant in the seed of a deliberately selected species; Pursh (1814) maintained that *Anthoxanthum odoratum* and *Festuca elatior* [probably *Lolium pratense* (Huds.) S. J. Darbyshire] arrived in this manner. Although the link between naturalization and the deliberate introduction of species for food, forage, and medicinal use continued, even in the 17th century some species appear to have been imported for aesthetic reasons. The list of species selected as ornamentals has expanded ever since; in fact, it dwarfed the number of new immigrant species in more utilitarian categories by at least 1860, if not earlier (Mack & Erneberg, 2002).

The link between agriculture in western Europe and the establishment of colonial agriculture was so strong that by ca. 1850, the weed and ruderal

floras of western Europe and eastern North America were quite similar. Through a combination of deliberate introductions and seed contaminants in imported seed and other cargo, Europe's colonizing flora had been largely transplanted to form much of North America's naturalized flora. Although formed by happenstance, this link remains.

As introduced species were traded or accidentally spread in commerce among the eastern colonies beginning in the 17th century, a few species became so widespread and naturalized that they formed invasions. Although the known list of apparently invasive species by 1800 is modest, other species were probably playing that role but were not described in terms that we can decipher as invasions. The frequency with which widespread and perhaps invasive species were reported through the first half of the 19th century suggests that these species' opportunity to spread and consequently proliferate was tied to the growth of all forms of commerce and the forms of transportation that fostered the spread of commerce.

Furthermore, the connection between which species received cultivation in their new range and those that became naturalized appears high (Mack & Erneberg, 2002). This historic link between cultivation and naturalization (Mack, 2000) provides an important harbinger for the future. If the history of plant naturalization between 1634 and 1860 is any guide, future naturalizations will be largely shaped by (1) the often idiosyncratic human motivations for importing alien species, (2) the degree of cultivation provided to these species upon their entry, and (3) human industry in transporting those species to many new locales and habitats in new ranges, thereby enhancing the opportunities for establishment on sites where they can persist without further human assistance.

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